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An experimental test and models of drift and dispersal processes of pallid sturgeon (Scaphirhynchus albus) free embryos in the Missouri River

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Abstract Free embryos of wild pallid sturgeon Scaphirhynchus albus were released in the Missouri River and captured at downstream sites through a 180-km reach of the river to examine ontogenetic drift and dispersal processes. Free embryos drifted primarily in the fastest portion of the river channel, and initial drift velocities for all age groups (mean=0.66–0.70 ms^{-1}) were only slightly slower than mean water column velocity (0.72 ms^{-1}). During the multi-day long-distance drift period, drift velocities of all age groups declined an average of 9.7% day^{-1}. Younger free embryos remained in the drift upon termination of the study; whereas, older age groups transitioned from drifting to settling during the study. Models based on growth of free embryos, drift behavior, size-related variations in drift rates, and channel hydraulic characteristics were developed to estimate cumulative distance drifted during ontogenetic development through a range of simulated water temperatures and velocity conditions. Those models indicated that the average free embryo would be expected to drift several hundred km during ontogenetic development. Empirical data and model results highlight the long-duration, long-distance drift and dispersal processes for pallid sturgeon early life stages. In addition, results provide a likely mechanism for lack of pallid sturgeon recruitment in fragmented river reaches where dams and reservoirs reduce the length of free-flowing river available for pallid sturgeon free embryos during ontogenetic development.

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Introduction

Drift and dispersal of free embryos and larvae are early life history characteristics widely recognized and common in many lotic fishes (Pavlov 1994; Oesmann 2003; White and Harvey 2003; Reichard et al. 2004; Martin and Paller 2008). With respect to water velocity and behavior during the early life stages, drift and dispersal can be active, passive, or include a combination of active and passive components

(Pavlov 1994; Pavlov et al. 2008). Knowledge of natural drift and dispersal dynamics is necessary for understanding factors influencing recruitment in lotic fishes. For example, fragmentation of rivers by dams and reservoirs disrupts natural drift and dispersal processes by reducing the amount of free-flowing riverine habitat downstream from spawn and hatch locations. If early life stages are obligate to riverine conditions and/or exhibit little to no survival in lentic habitats, reservoirs at the drift terminus may act as recruitment sinks and jeopardize persistence of the population (Dudley and Platania 2007; Kynard et al. 2007; Braaten et al. 2008). Similarly, recruitment can be negatively affected if free embryos or larvae drift from productive spawn and hatch locations to thermally or hydrologically altered downstream reaches where survival is minimal (Robinson et al. 1998). In addition, increased water velocities and reduced heterogeneity resulting from river channelization affect natural drift and dispersal processes by increasing transport velocity, reducing the likelihood of localized settlement of larvae from the drift, and increasing cumulative distance drifted during ontogenetic development (Bond et al. 2000; Schiemer et al. 2001; Konecna et al. 2009). Quantification of dispersal and cumulative distance drifted during ontogenetic development in lotic systems requires integrating aspects of behavior, drift characteristics, and river channel hydraulics; however, it is recognized that few studies have examined these variables simultaneously (Bond et al. 2000; Dudley and Platania 2007), especially with respect to understanding drift and dispersal of early life stages in large rivers across broad spatial scales.

The pallid sturgeon, Scaphirhynchus albus, is endemic to the Missississippi River basin including the Missouri River from Montana to Missouri, the middle and lower Mississippi River downstream from the confluence of the Missouri River, and larger tributaries entering these systems (Bailey and Cross 1954). The pallid sturgeon is listed as an endangered species in the United States (Dryer and Sandvol 1993) and is recognized under the Convention on International Trade in Endangered Species (CITES; Pikitch et al. 2005). A variety of anthropogenic factors including habitat alterations (e.g., river fragmentation resulting from dam construction, flow alterations, channelization) have been implicated in the demise of pallid sturgeon populations (USFWS 2000), negatively influencing reproduction and recruitment.

In the upper and middle portions of the Missouri River, a series of six large mainstem dams have transformed the once free-flowing river into an alternating sequence of reservoirs separated by short lengths of free-flowing river. The greatest length of free-flowing river (340 km) between dams and the next downstream reservoir occurs in the uppermost portion of the Missouri River between Fort Peck Dam in Montana (dam closed in 1937) and Lake Sakakawea (impounded by Garrison Dam in North Dakota, dam closed in 1953). The Yellowstone River (longest free-flowing river in the conterminous United States; Galat et al. 2005) enters the Missouri River about 25 km upstream from Lake Sakakawea, and provides near-natural discharge and thermal regimes to the Missouri River. An extant population of about 160 wild adult pallid sturgeon (Klungle and Baxter 2005) comprised predominantly of large (>1100 mm; USFWS 2006) and presumably old individuals (>40 years; Keenlyne and Jenkins 1993) is present in this portion of the Missouri River and Yellowstone River, but has declined over the last several decades (Braaten et al. 2009a). Although spawning occurs (Fuller et al. 2008), there has been no documented natural recruitment in this population for decades.

Much of the recent emphasis for identifying the mechanism of recruitment failure in this reach of the Missouri River has focused on the free embryo and larval life stages of pallid sturgeon, and this emphasis is justified given that a lack of recruitment, despite successful spawning, suggests a recruitment bottleneck during the early life stages. Laboratory (Kynard et al. 2002a, 2007) and small-scale field studies (Braaten et al. 2008) indicate that pallid sturgeon free embryos initiate downstream drift immediately after hatching, and may drift for several hundred km during the initial 9–11 day post-hatch (dph) dispersal period. These studies provide support to the hypothesis that recruitment failure of pallid sturgeon is linked to a mismatch (Kynard et al. 2007) between long-distance drift and dispersal requirements of the early life stages and the reduced length of free-flowing lotic habitat in the contemporary Missouri River. However, it is unknown if patterns and inferences from laboratory and small-scale field studies are applicable to large river conditions as large river channels exhibit substantial heterogeneity (e.g., greater depths and velocities and ranges of these variables, islands and sand bars, large pools and eddies) that may influence drift and moderate drift patterns during the early life stages of pallid sturgeon.

Expanding on previous laboratory studies (Kynard et al. 2002a, 2007) and small-scale field experiments (Braaten et al. 2008), this large-scale experimental study assessed multiple objectives related to the drift and dispersal of pallid sturgeon free embryos throughout a 177-km reach of the mainstem Missouri River. The first objective tested the hypothesis that 5–13 dph pallid sturgeon exhibit downstream drift and dispersal when subjected to river conditions characteristic of their native habitat. The second objective examined drift velocity of free embryos relative to mean water column velocity, and compared drift velocity among different ages and lengths. We used modeling in the third objective to estimate the cumulative distance drifted by pallid sturgeon free embryos during ontogenetic development through a range of water temperatures (14, 16, 18, 20, 22, 24°C) and mean velocity conditions characteristic of the Missouri River (0.50–0.90 ms^{-1}). Whereas simulations involving moderate to warm temperatures (18–24°C) represent natural thermal conditions during which spawning and drift likely occurred in the Missouri River prior to anthropogenic alterations, simulations involving low temperatures (14°C, 16°C) are representative of altered conditions in the contemporary river. Drift distance models based on interactions involving behavior, development, and river channel hydraulic factors were compared to models based exclusively on passive, velocity-driven transport of free embryos. Results obtained from the third objective provided inferences on a mechanism for the lack of pallid sturgeon recruitment in the upper Missouri River, where river fragmentation has reduced the length of free-flowing habitat necessary for ontogenetic development.

Methods

Study area

The Missouri River study area is located in eastern Montana and western North Dakota within a river reach extending from Fort Peck Dam at river km (rkm; distance upstream from the confluence of the Missouri River and Mississippi River) 2850 to the confluence of the Yellowstone River at rkm 2547 (Fig. 1). The river channel (slope=0.0002) is 240–380 m wide within a floodplain valley 2.0–6.5 km wide (Darby and Thorne 2000; Shields et al. 2000; Simon et al. 2002). Mean annual discharge is 278 $m^3\ s^{-1}$ for the years 1943–2007 (Ladd 2008; USGS gage number 06177000 located at rkm 2,739; Fig. 1); however, discharge throughout the reach results primarily from regulated hypolimnetic releases through Fort Peck Dam with periodic inputs from tributaries augmenting flows released from the dam. Operations of Fort Peck Dam have reduced peak flows that naturally occurred in spring and early summer, and highest flows under contemporary operations typically occur later in the year (Galat and Lipkin 2000; Bowen et al. 2003). Hypolimnetic releases from the dam suppress water temperatures relative to the free-flowing Missouri River upstream from the dam and adjacent free-flowing rivers (i.e., Yellowstone River; Galat et al. 2005; Braaten et al. 2009b). Despite regulated flow conditions, this section of the Missouri River retains a semblance of a relatively natural river channel as in-channel anthropogenic alterations are minimal. Islands, secondary channels, and sand bars are common throughout the reach (Shields et al. 2000; Bowen et al. 2003), and provide heterogeneity to main channel habitat. However, in association with suppression of high flows, dam construction and operation have caused channel degradation (Shields et al. 2000; Simon et al. 2002) resulting in the isolation of some historical side channels from the existing main channel. Water column velocity averages 0.60–0.80 ms^{-1} and average depth is 2–3 m (Galat et al. 2001). Sand is the dominant substrate throughout the reach (~ 90%; Galat et al. 2001), although gravel and cobble are present especially in the upper reaches close to Fort Peck Dam (Shields et al. 2000; Galat et al. 2001). Within the reach between Fort Peck Dam and the Yellowstone River, the study area was concentrated in a 177.0 km section of the Missouri River between rkm 2739 and rkm 2562 (Fig. 1)

Source of pallid sturgeon free embryos

Pallid sturgeon free embryos used in the drift studies were produced from wild brood stock captured in the Yellowstone River and Missouri River downstream from the Yellowstone River confluence (Fig. 1), and spawned artificially in hatcheries during 20–27 June

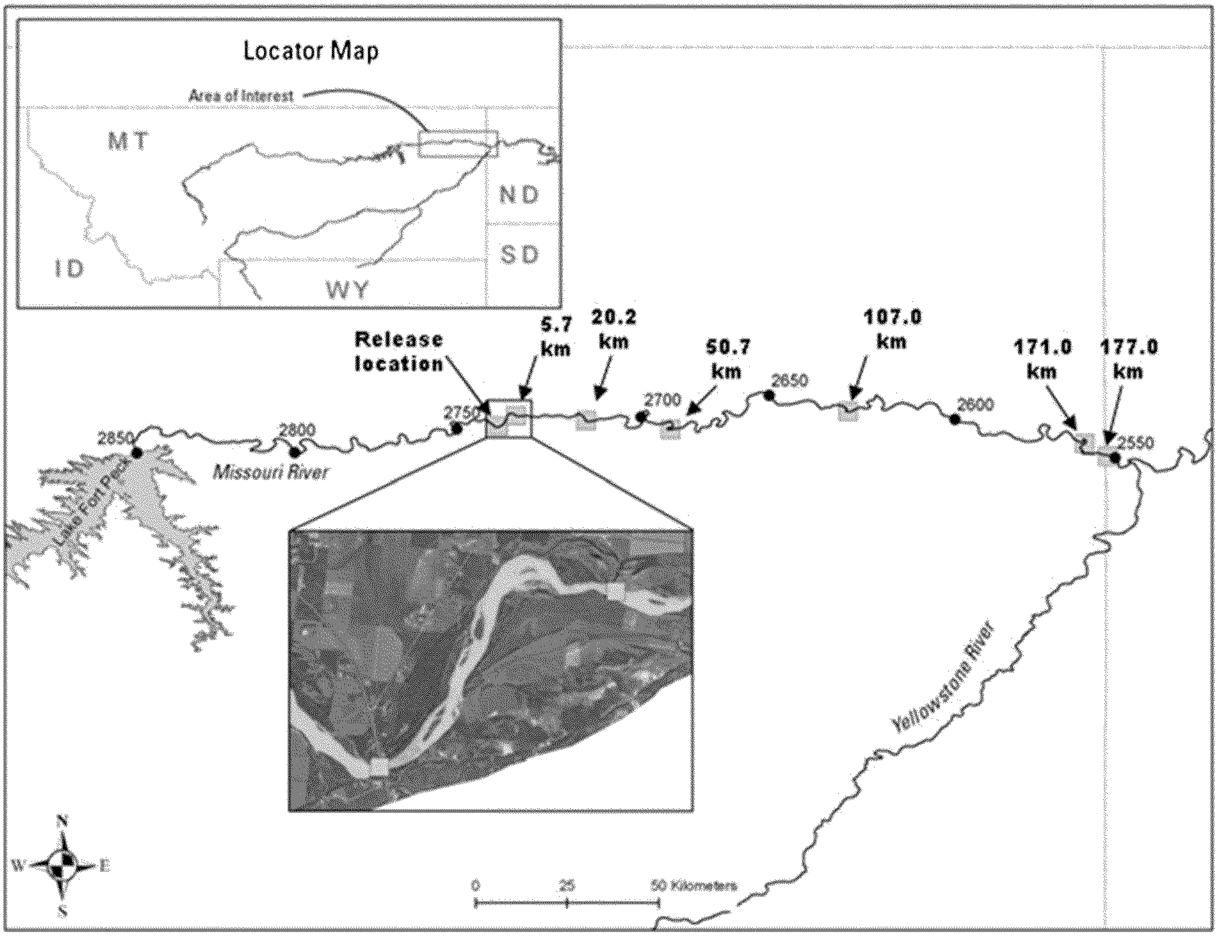

Fig. 1 Map of the Missouri River study area highlighting river km (solid circles) and pallid sturgeon release and capture locations (shaded squares; km downstream from the release location). The inset map details the initial 5.7 km of the study area showing the release location and 5.7 km sampling location

2007 as part of the pallid sturgeon conservation propagation program (USFWS 2006). The mating, incubation, and rearing process was used to produce a total of 428 285 free embryos comprised of 182 018 5-dph individuals, 41 885 6-dph individuals, 101 777 10-dph individuals, 32 724 12-dph individuals, and 69 881 13-dph individuals (Table 1). All age groups with the exception of 10-dph free embryos contained progeny of mixed genetics as multiple males were used to fertilize eggs from one or more females. The 10-dph group was produced from a single male and single female. Incubation and rearing was conducted at the U. S. Fish and Wildlife Service Garrison Dam National Fish Hatchery (GDNFH; Riverdale, North Dakota). Embryos produced from spawning events at the U. S. Fish and Wildlife Service Gavins Point National Fish Hatchery (GPNFH; Yankton, South Dakota) were transported to GDNFH for incubation and rearing of young. Numbers of pallid sturgeon for each age group were estimated volumetrically by determining the number of individuals per ml from a subsample, and extrapolating this estimate to the total volume of free embryos. Due to normal variation in incubation and hatch times, ages for each age group represented average dph. All pallid sturgeon were packaged in plastic bags at GDNFH on the morning of 9 July, and transported in coolers via truck to the study site release location at rkm 2739. All age groups appeared healthy and active upon arrival at the study site. Bags containing pallid sturgeon free embryos were placed in the river and river water was added gradually over a 30-min time period to acclimate free embryos to the river temperature (19.6°C). When free embryos were within 1°C of

Table 1 Wild brood stock (identified by passive integrated transponder number; PIT), age classes (mean days post-hatch; dph), and pre-release thermal exposure (cumulative thermal units, CTU; sum of mean daily water temperature) of pallid sturgeon free embryos released in the Missouri River on 9 July 2007

Female PIT	Male PIT	Mean age (dph)	CTU	Number released
40636B2945	4443422E34	5	79	6140
40636B2945	115712453A	5	79	34 629
47037F460C	1F4A5A5A63	5	79	37 712
47037F460C	454B30016B	5	79	66 104
47037F460C	7F7F066471	5	79	37 433
47151A3D3A	1F4A363031	6	95	10 179
47151A3D3A	7F7D372A6B	6	95	11 250
47151A3D3A	115669294A	6	95	20 456
4443240458	132157621A	10	158	101 777
115553544A	115556461A	12	191	6900
115553544A	4441774C6E	12	191	10 904
470378405D	115556461A	12	191	7838
470378405D	1F4A34194A	12	191	7082
7F7B025D51	4441774C6E	13	207	14 978
7F7B025D51	1F5001721E	13	207	23 240
7F7B025D51	7F7D41431D	13	207	31 663
				428 285

river temperature, free embryos were transferred to a common tank in preparation for release.

Sampling design and protocols

At 16:30 h on 9 July, pallid sturgeon free embryos were released en masse at rkm 2739 in the middle of the river channel at the water surface. Drift sampling was initiated on 9 July during late afternoon and continued through early evening at a site 5.7 km downstream from the release location. Based on detailed water velocity information for the 5.7 km reach (see below), it was determined that drifting pallid sturgeon would require at least 1-h of travel time to drift from the release site to the initial collection site if free embryos drifted at maximum water velocity. Thus, sampling at the 5.7 km location was initiated 1 h post release.

Based on travel time and drift velocity of the leading edge of the drifting population at the 5.7 km location, we estimated the distance (km) that pallid sturgeon would drift in a specified amount of time and this information was used to establish subsequent downstream sampling locations and sampling times. Following this protocol, sampling at downstream locations was initiated 1–2 h prior to the predicted arrival time of the leading edge of the drifting population to ensure that the leading edge of the population had not passed prior to our predicted time. Based on travel time and travel distance predictions, subsequent sampling locations were established for the night of 9 July and early morning on 10 July (20.2 km downstream from the release location), during the day on 10 July (50.7 km downstream from the release location), during the day on 11 July (107.0 km downstream from the release location), during the day on 12 July (171.0 km downstream from the release location), and during the day on 13 July (177.0 km downstream from the release location; Fig. 1).

Protocols for sampling pallid sturgeon at the 5.7 km location are outlined in Braaten et al. (2010). Four boats were positioned at different lateral locations across the river channel including the inside bend (ISB), the inside bend channel border (ISB-CHNB), mid-channel (MID-CHNL) in the thalweg, and outside bend (OSB) in the thalweg. Boats positioned at the ISB and MID-CHNL locations sampled drifting pallid sturgeon using a rectangular frame net (0.5 m height, 0.75 m width, 3.0 m long, 1000 μm mesh) deployed from one side of the boat and a conical net (0.5 m diameter, 1.5 m long, 750 μm mesh) deployed from the opposite side of the boat. Both net types at these locations were fished simultaneously adjacent to bottom with the lower frame of the net resting on the river bed. At the ISB-CHNB and OSB locations, conical nets as described above were used but one conical net was fished on the bottom while the other conical net was deployed simultaneously from the opposite side of the boat and fished in the upper 0.5 m of the water column. Nets at all locations were fished for 5-min, the cod-end collecting cup was quickly removed and replaced, and nets were immediately redeployed for the next 5-min sampling period. Thus, sampling was nearly continuous except for a 15–20 s time period during each 5-min interval when the net was retrieved, the cod-end cups were removed and replaced, and the net was redeployed. Sampling continued until catches declined to zero. Sample contents were fixed in a 10% buffered formalin solution for later processing in the laboratory. All nets were equipped with a flow meter from which water velocity and volume of water sampled could be estimated. The sampling regime implemented at the 5.7 km location was used to assess the 2-dimensional (lateral, vertical) drift characteristics of pallid sturgeon (Braaten et al. 2010) and provide guidelines for sampling larvae at subsequent downstream locations. A crew of 4–5 individuals was stationed in each boat.

Based on the findings that free embryos at the 5.7 km location drifted almost exclusively (≥98%) in the lower 0.5 m of the water column and concentrations were greatest in the thalweg (Braaten et al. 2010), sampling at locations downstream from the 5.7 km site was conducted in the thalweg using rectangular frame nets (described above) fished in the lower 0.5 m of the water column adjacent to the river bed. A single boat with 2–3 crew members was used at the downstream locations. Sampling was conducted for 5-min with the exception of 12 July (171.0 km downstream) when sampling was increased to 10-min for some samples in an effort to increase sample volume and increase the likelihood of capturing pallid sturgeon after free embryos did not occur in the drift as predicted (see Results). In contrast to the 5.7 km site, sampling at downstream sites was not continuous as a 10–30 min processing period was required between samples to extract and enumerate free embryos from the previous samples.

In the laboratory, pallid sturgeon from sample-site and time-specific collections were extracted from detritus and enumerated. Total length (nearest 0.1 mm) was measured using an ocular micrometer embedded in a stereomicroscope. Individuals that were broken, torn, or otherwise deformed were not measured, but were included as part of the total catch for a sample. Catches of drifting pallid sturgeon through time (hours post-release) at sites 5.7, 20.2, 50.7, 107.0, 171.0 and 177.0 km downstream from the release site were expressed as drift concentration (number of free embryos m^{-3}).

River velocities and environmental conditions

Detailed water velocity data were collected in the initial river reach spanning from the release point to the 5.7 km sampling location (Fig. 1). A total of 27 transects perpendicular to the flow was established at 200 m intervals throughout the reach. Using an acoustic Doppler current profiler (ADCP; Shields et al. 2003), each transect was traversed perpendicular to the flow to obtain velocity data. The ADCP measurements were obtained for 13 transects on 27 June and 14 transects on 28 June at discharges of 201.0 $m^3 s^{-1}$ and 203.9 $m^3 s^{-1}$, respectively. These discharges are less than the long-term (1943–2007) mean July discharge (285 $m^3 s^{-1}$) for this reach of the Missouri River (Ladd 2008).

Whereas the ADCP data provided detailed information on mean water column velocity in the initial portion of the study area, additional information on mean water column velocity was needed to determine how water velocity changed from upstream to downstream within the drift reach and subsequently estimate velocities to which drifting free embryos were exposed during the downstream drift period. Data were compiled from USGS gage stations at the release location (gage number 06177000) and at rkm 2609 (gage number 06185500, 130 km downstream from the release location). Using linear regression, a relationship was established between mean water velocity and discharge for a range of discharges common to both sites between 2004 and 2009 (upstream gage, 115–267 $m^3 s^{-1}$; downstream gage, 114–270 $m^3 s^{-1}$).

Water temperature was measured at multiple sites between the release location and final collection location by a series of water temperature loggers programmed to record temperature at 1-hr intervals. Turbidity (nephelometric turbidity units; NTU) was measured at the collection locations.

Statistical analysis

A Kruskal-Wallis test was used to compare drift velocity (m s^{-1}) among age groups of free embryos. Models developed to estimate cumulative distance drifted by pallid sturgeon during ontogenetic development required multiple input variables obtained from earlier objectives and other studies (as described below). First, univariate statistics were used to quantify empirical drift velocity distributions for each age and length group including the mean drift velocity exhibited by the population and the following quantiles of the drift velocity distributions: minimum velocity, 1%, 5%, 10%, 25%, 75%, 90%, 95%, 99%, maximum velocity. These descriptive statistics were used to express drift velocity relative to mean water column velocity in the river channel. For example, if the maximum observed drift velocity exhibited by a specific age group was 0.83 ms^{-1} and mean water column velocity was 0.72 ms^{-1}, then the fastest drifter in the population was dispersing at a rate of 1.153 times greater mean water column velocity. Similarly, if the 5% quantile of the drift velocity distribution was 0.63 ms^{-1}, then it could be established that the 5% portion of the drifting population was dispersing at a rate of 0.875 times less than mean water column velocity. This process was conducted for all quantiles of the drift velocity distributions for each age and length group. Although pallid sturgeon less than 5 dph were not used in this study, drift velocities for younger ages are similar to or just slightly faster than 5 dph larvae (Braaten et al. 2008). Thus, drift velocity characteristics for 5 dph free embryos observed in this study were used to quantify drift rates of younger larvae. Drift velocity characteristics for other age groups not examined in this study (i.e., 7, 8, 9, 11 dph) could be inferred from collections after the initial release date as pallid sturgeon increased in age and length during the multiple-day downstream drift period. Based on the technique above, estimates of drift rate relative to mean water column velocity spanning from the slowest to the fastest drifters in the population were available for of all age groups.

The second step in the process for estimating cumulative drift distance during ontogenetic development required establishing the relationship between water temperature and development of free embryos, and using this information to estimate when free embryos transition from endogenous to exogenous feeding larvae, and transition from drifting to settlement in benthic habitats (Kynard et al. 2007). The yolk sac of free embryos is absorbed after exposure to about 200 cumulative thermal units (CTU; sum of mean daily water temperature for each day of life after hatching) at a length of 18–19 mm (Snyder 2002; Kynard et al. 2007; Braaten et al. 2008). Based on this information and knowledge of length at hatch (8.5 mm, reported as 8–9 mm by Snyder 2002), growth of free embryos and duration (number of days) of the drifting life stage were estimated for six water temperature regimes (14, 16, 18, 20, 22, 24°C) by the following process:

Growth from hatch to length at initiation of settlement:

$$18.0\,\text{mm (initiation of settlement)} - 8.5\,\text{mm (mean hatch length)} = 9.5\,\text{mm} \quad (1)$$

Thermal growth capacity (TGC):

$$9.5\,\text{mm divided by } 200\,\text{CTU (required for yolk absorption)} = 0.0475\,\text{mm}\,\text{CTU}^{-1} \quad (2)$$

The length increment grown during each day of life could be estimated by multiplying 0.0475 mm CTU^{-1} (Eq. 2) by the specific water temperature of interest. For each water temperature regime, this process was additive for each day of life until 9.5 mm of growth (Eq. 1) was achieved to attain a total length of 18.0 mm (length at initiation of settlement). The process yielded an estimate of the number of days free embryos would be expected to drift (Kynard et al. 2007) as illustrated by the following example. At the modeled exposure temperature of 18°C, an estimated 0.86 mm of growth was attained each day. The total length increment attained after 11 days of exposure to 18°C was 9.46 mm, similar to the 9.5 mm of growth necessary to attain 18.0 mm. Thus, for the modeled 18.0°C water temperature regime, free embryo pallid sturgeon would be expected to drift for 11 days. The growth information was also used as the basis for assigning age- and length-specific drift velocities to free embryos as they drifted downstream and developed. Cumulative distance drifted during ontogenetic development (km) was modeled for mean water velocities of 0.50–0.90 ms^{-1}. In addition to developing cumulative drift distance models based on drift behavior and channel hydraulics, cumulative drift models based exclusively on passive transport by mean water velocity were also developed. The passive drift models served as a template for comparisons to cumulative drift models based on empirical drift information for pallid sturgeon free embryos.

Results

Hydrologic conditions

Mean water column velocity between the release location at rkm 2739 and the initial collection location 5.7 km downstream was 0.72 ms^{-1} (S.D. = 0.06 m s^{-1}, n=27 transects) for ADCP velocity data collected at discharges of 201.0–203.9 m^3 s^{-1} on 27 June and 28 June. On 9 July when pallid sturgeon free embryos were initially released, discharge at the release site had decreased about 12% to 177.4 m^3 s^{-1}. Pallid sturgeon free embryos were exposed to slightly greater discharges during the downstream drift period as the gage located at rkm 2,609 recorded discharges of 185.4–193.0 m^3 s^{-1} between 11 and 13 July. Mean water column velocity increased significantly with increasing discharge based on gage data at the release site (r^2=0.64, P=0.0004, n=15, equation: m s^{-1}= 0.49+0.0012 m^3 s^{-1}) and for the gage located 130 km downstream from the release site (r^2=0.66, P= 0.0013, n=12, equation: m s^{-1}=0.54+ 0.0011 m^3 s^{-1}). However, through the range of discharges examined, velocity was slightly greater at the downstream location suggesting that mean water column velocity may increase in the downstream reaches. Although water temperature at time of release was 19.6°C, mean daily temperature averaged 20.8°C (range 18.8–22.5°C) through 13 July at sites downstream. Turbidity on the day of release was 25.7 NTU, but free embryos were exposed to higher turbidity (72.9–75.2 NTU) as they drifted downstream through 13 July.

Drift concentrations of pallid sturgeon free embryos

Drift of pallid sturgeon free embryos occurred primarily in the fastest and deepest areas of the river channel as indicated by intensive sampling at the 5.7 km sampling location. Greater than 95% of the free embryos sampled at this location were collected at the MID-CHNL (n=2081) and OSB (n=1259) locations. The ISB-CHNB and ISB locations yielded 102 and 41 free embryos, respectively.

Pallid sturgeon free embryos sampled at the 5.7, 20.2 and 50.7 km locations exhibited a pattern of initial arrival to the sampling locations, an increase in concentration to maximum levels, then a decline in concentration as occurrence in the drift diminished (Fig. 2). A similar pattern occurred at the 107.0 km sampling location, but maximum concentration had not reached the site when sampling was terminated. The number of free embryos collected in the drift declined, concentrations decreased, and catch distributions broadened as the free embryo population drifted downstream (Fig. 2). At 171.0 km downstream from the release point, no pallid sturgeon free embryos were sampled between 67.8 and 73.0 h post-release despite the prediction that they would be present in the drift. Sampling conducted 177.0 km downstream from the release site (87.8–92.2 h post release) yielded 13 pallid sturgeon free embryos, but it could not be determined if the concentrations represented the leading edge just following initial arrival of larvae, the prolonged period of elevated concentrations leading up to maximum concentration, or the trailing edge of the drifting population when concentrations would be low.

Size composition and drift velocity of free embryos

Overlap in maximum length and minimum length of adjacent age classes existed making it difficult to delineate exact lengths of each age group. As a result, 5–6 dph free embryos were combined for the analysis

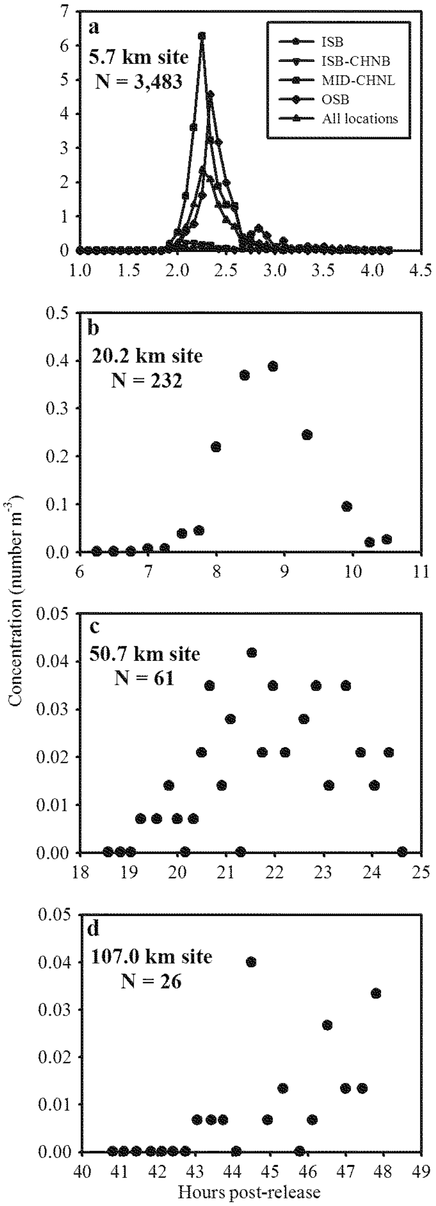

Fig. 2 Concentrations (number of free embryos m^{-3}) of pallid sturgeon through time (hours post-release) at sampling locations in the Missouri River. a concentrations 5.7 km downstream from the release location by boats positioned on the inside bend (ISB), inside bend channel border (ISB-CHNB), mid-channel (MID-CHNL), outside bend (OSB), and averaged across all locations, b concentrations 20.2 km downstream from the release location, c concentrations 50.7 km downstream from the release location, d concentrations 107.0 km downstream from the release location. N = total number of free embryos sampled at each site. Note change in the abscissa and ordinate values among graphs

as were 12–13 dph free embryos (Table 2). Although all age groups were represented through the 107.0 km drift distance, the occurrence of older age groups was minimal at the 107.0 km location. Pallid sturgeon originally released as 5–6 dph and 10 dph free embryos exhibited progressions in mean length during the downstream drift period and expressed a growth rate of about 0.85 mm day^{-1} (based on 1.72 day cumulative travel time of leading edge). Free embryos originally released as 12–13 dph did not exhibit consistent progressions in mean length and maximum length only slightly exceeded 20.0 mm on any collection occasion. These results suggest that the transition from drifting (free embryos) to settling (larvae) was occurring between 18.0 and 20.0 mm. The 13 pallid sturgeon free embryos collected 177.0 km downstream from the release site were used for genetic analysis and length measurements. Eleven free embryos were preserved in ethanol immediately after collection for genetic analyses, and two individuals (17.2 mm, 17.5 mm) were fixed in formalin. Genetic analyses indicated that the 11 free embryos originated from the genetic population of free embryos originally released as 5 dph (P. DeHaan, U. S. Fish and Wildlife Service, Abernathy Fish Technology Center, Conservation Genetics Laboratory, Longview, Washington, pers. comm.). Thus, these pallid sturgeon were nearly 9 dph when collected from the drift. The free embryos preserved in formalin were similar in size to those used in genetic analysis, suggesting that all free embryos sampled on 13 July represented individuals originally released at 5 dph.

Drift velocities of pallid sturgeon at the initial 5.7 km sampling site differed significantly among age groups (Kruskal-Wallis test, $P<0.0001$) as drift rates were fastest for 5–6 dph free embryos (Table 2). Across all age groups, mean drift velocities were only slightly less than mean water column velocity (0.72 m s^{-1}) in the Missouri River. Statistical comparisons of drift velocity among age groups could not be conducted for other locations because collections did not span the entire period of occurrence in the drift (Fig. 2) and slower drifting individuals would have an influence on estimates of central tendency and variability. However, velocity of the leading edge of the drifting population (maximum drift velocity) declined significantly with increasing drift distance (Fig. 3). Exclusion of an outlying data point (representing 11 dph pallid sturgeon 50.7 km downstream

Table 2 Attributes for length (mm; mean, standard deviation, S.D.; minimum, Min.; maximum, Max.) and drift velocity (m s^{-1}; mean, S.D., Min., Max.) and sample size (N) for pallid sturgeon free embryos sampled 5.7, 20.2, 50.7 and 107.0 km downstream from the release location in the Missouri River. Mean, S.D., and minimum drift velocity for free embryos past the 5.7 km location could not be determined because the entire drift distribution was not sampled

			Length (mm)				Drift velocity (m s^{-1})			
Sampling location (km)	Age group (dph)	N	Mean	S.D.	Min.	Max.	Mean	S.D.	Min.	Max.
5.7	5–6	1,361	13.6	0.5	11.1	14.8	0.70	0.05	0.48	0.83
	10	530	15.8	0.4	14.9	16.9	0.66	0.05	0.53	0.79
	12–13	1,422	19.2	0.5	17.1	20.5	0.66	0.08	0.39	0.83
20.2	5–6	162	13.9	0.4	12.3	14.6				0.75
	10	14	16.0	0.4	15.4	16.3				0.77
	12–13	45	19.3	0.5	18.3	20.2				0.80
50.7	6–7	36	14.1	0.4	13.0	14.9				0.71
	11	4	16.2	0.3	15.9	16.6				0.59
	13–14	19	19.2	0.7	17.8	20.3				0.73
107.0	7–8	22	15.3	0.5	13.6	16.0				0.69
	12	2	17.0	0.1	16.9	17.1				0.67
	14–15	1	20.0							0.67

from the release point) improved model fit, but the trend was similar to the original model (Fig. 3). Expressed on a daily basis, drift velocity declined at an average rate of 9.7% day^{-1} between collections at the 5.7 km location and 107.0 km location. Based on declining velocity with increasing drift distance, predictions from the regression model suggested that the leading edge of the drifting population would have arrived 171.0 km downstream from the release site on 12 July at a cumulative drift rate of 0.59 ms^{-1}. This prediction lends support to empirical data which indicated that drift rates of pallid sturgeon had declined to less than 0.65 ms^{-1} at the 171.0 km location based on the period of sampling conducted at this location. Collections of pallid sturgeon free embryos at the 177.0 km location on 13 July indicated that at least a portion of the population was drifting at 0.53–0.56 ms^{-1}.

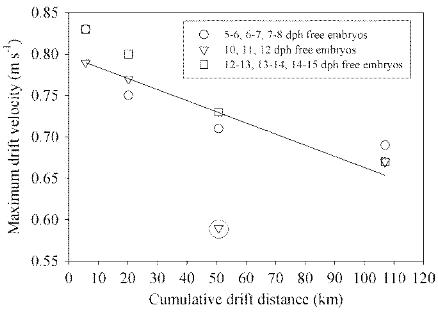

Fig. 3 Change in maximum drift velocity (m s^{-1}) of pallid sturgeon drifting among sites 5.7, 20.2, 50.7, and 107.0 km downstream from the release location. The model inclusive of all data points was significant (r^2=0.56, P=0.005, n=12). The model excluding an outlying data point (identified as the circled triangle) was significant (r^2=0.86, P<0.0001, n=11)

Cumulative drift distance of pallid sturgeon free embryos

Models of cumulative distance drifted by pallid sturgeon free embryos including a 9.7% day^{-1} decrease in drift velocity indicated that drift distance was lowest at high water temperatures due to reduced duration of the drift period that occurred at higher water temperatures (Fig. 4; Table 3). Model estimates of cumulative drift distance based exclusively on passive transport of free embryos drifting under a constant rate of mean channel velocity were much greater than cumulative drift distance models that incorporated behavioral components and slowing drift rate with increasing drift distance (Fig. 4).

Discussion

Pallid sturgeon exhibit an innate behavior to enter the drift and disperse in the water column immediately

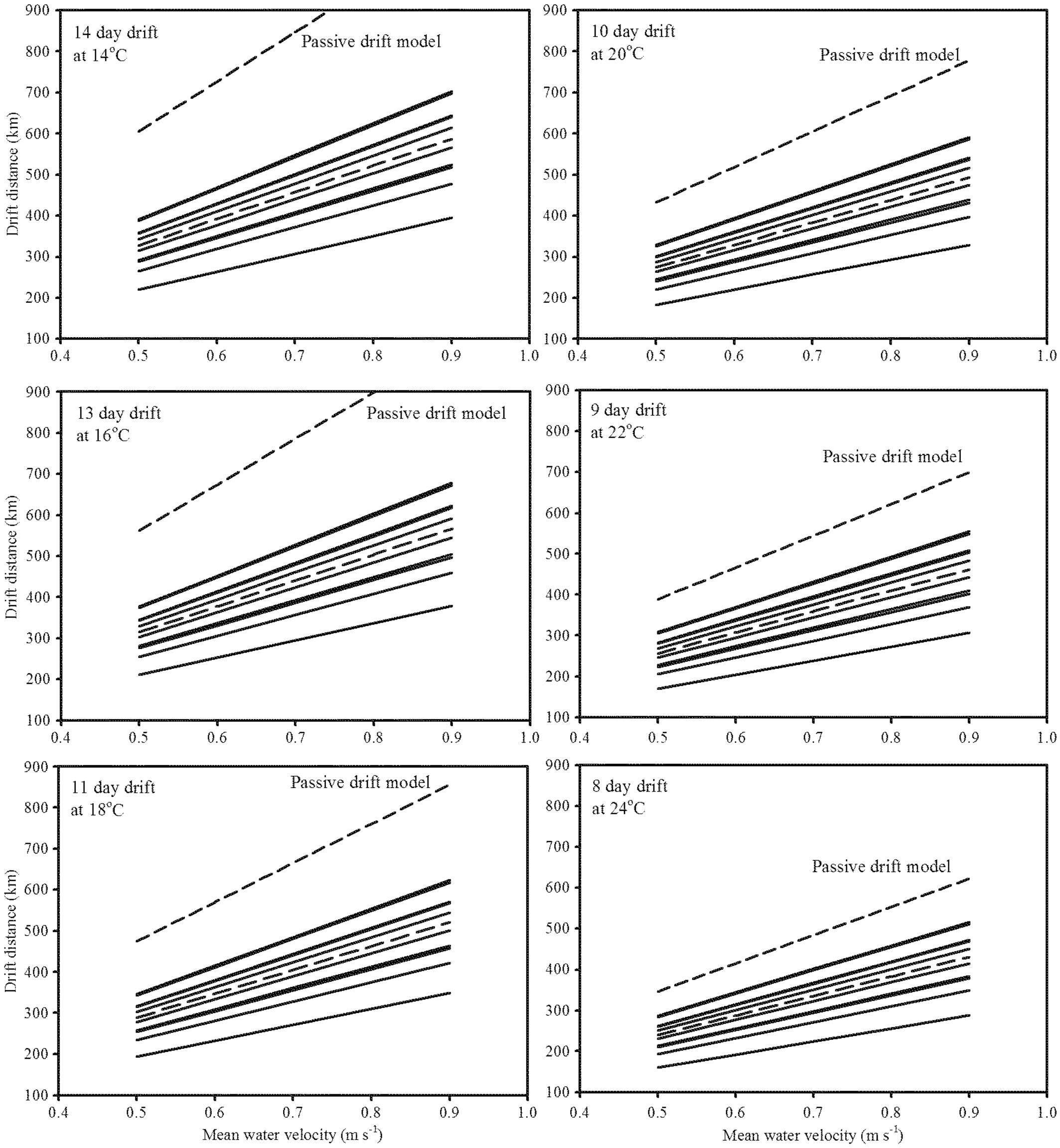

Fig. 4 Predicted cumulative drift distance (km) of free embryo pallid sturgeon as a function of mean water column velocity (0.50–0.90 ms^{-1}) at six water temperature regimes (14, 16, 18, 20, 22, 24°C). The uppermost dashed line in each graph represents estimated drift distance based on passive transport of free embryos drifting at mean water column velocity for the entire drift duration (i.e., passive drift model). Groups of lines within each graph depict the range of drift distances exhibited by the population corresponding to distribution quantiles (maximum distance, 99%, 95%, 90%, 75%, mean (dashed line for reference), 25%, 10%, 5%, 1%, minimum distance). Note that duration (days) of the larval drift period declines as water temperature increases

after hatch (Kynard et al. 2002a, 2007). This behavior has been reported in earlier sturgeon investigations (Deng et al. 2002; Kynard et al. 2002a, b; Zhuang et al. 2002; Gisbert and Ruban 2003; Zhuang et al. 2003; Kynard and Parker 2005; Braaten and Fuller 2007), but differs from other sturgeon studies (Auer and Baker 2002; Deng et al. 2002; Kynard and Horgan 2002; Kynard and Parker 2004; Kynard et al. 2005; Smith and King 2005) where free embryos remain in the substrate after hatching. After entering the drift, pallid sturgeon free embryos drift primarily in the lower strata of the water column (Kynard et al.

Table 3 Model parameters (intercept, slope) for Fig. 4 quantifying the cumulative drift distance distribution (mean, distribution quantiles) of pallid sturgeon drifting at 14°C for 14 days, 16°C for 13 days, 18°C for 11 days, 20°C for 10 days, 22°C for 9 days and 24°C for 8 days. The model is of the form: Y ¼ a þ bx, where Y = km, a = intercept, b = slope, and x = mean water velocity in m s^{-1}. Model parameters were generated for water velocities ranging from 0.50 ms^{-1} to 0.90 ms^{-1}

Drift distance variable	Intercept	Slope	Intercept	Slope	Intercept	Slope
	14°C, 14 day drift		16°C, 13 day drift		18°C, 11 day drift	
Maximum	−0.0007	780.853	−0.0017	754.413	−0.0007	692.703
99%	−0.0003	774.827	0.0007	747.737	−0.0004	686.888
95%	a	715.160	0.0003	690.943	0.0007	634.425
90%	0.0010	710.640	−0.0010	685.940	0.0003	630.065
75%	−0.0004	682.200	0.0007	658.457	−0.0005	604.833
Mean	−0.0003	652.355	−0.0010	629.430	b	578.250
25%	−0.0008	628.874	0.0003	606.103	−0.0003	557.067
10%	0.0005	582.143	−0.0003	560.957	0.0004	515.612
5%	−0.0002	574.612	0.0003	552.615	−0.0003	508.345
1%	−0.0010	530.770	0.0010	509.420	c	468.990
Minimum	0.0007	438.265	0.0003	421.525	0.0004	387.742
	20°C, 10 day drift		22°C, 9 day drift		24°C, 8 day drift	
Maximum	0.0010	656.790	0.0005	617.023	0.0005	572.983
99%	−0.0005	650.353	0.0004	609.892	−0.0007	567.993
95%	−0.0003	601.537	−0.0003	565.115	f	524.780
90%	−0.0004	596.708	−0.0005	559.767	−0.0002	521.036
75%	0.0004	572.782	e	537.290	0.0005	500.163
Mean	−0.0008	547.364	−0.001	513.160	0.0008	478.132
25%	0.0005	526.583	−0.0005	492.827	−0.0003	460.475
10%	−0.0010	487.280	0.0010	455.900	−0.0003	426.185
5%	d	479.230	0.0005	446.987	−0.0003	419.945
1%	0.0007	441.005	0.0007	410.015	0.0008	387.212
Minimum	−0.0003	365.575	0.0003	341.025	0.0003	320.323

[a] 1.09×10^{-12}

[b] 2.94×10^{-15}

[c] -4.57×10^{-13}

[d] -8.5×10^{-13}

[e] -1.8×10^{-13}

[f] 1.08×10^{-12}

2007; Braaten et al. 2008; Braaten et al. 2010), alternate between brief periods of active swim-up followed by passive sinking (Kynard et al. 2007), and exhibit extended downstream drift and dispersal behaviors when subjected to relatively natural habitat and hydraulic conditions characteristic of the main-stem Missouri River. In addition, downstream drift and dispersal were continuous processes on a diel cycle as drifting free embryos were present in the drift during day and night. Expression of continuous drift behavior facilitated an accurate prediction of when larvae would arrive at the next downstream location, except when longitudinal decreases in drift velocity cumulatively slowed the drifting population as evidenced on 12 July when free embryos did not arrive at the 171.0 km downstream sampling location. Kynard et al. (2007) similarly found that the free embryos and larval life stages of pallid sturgeon drifted during day and night, but also presented evidence for slight variations in diel drift characteristics for specific ages. In contrast to pallid sturgeon, other sturgeon species exhibit cyclical periods of drift activity. For example, drift of larval lake sturgeon A. fulvescens is primarily nocturnal (D'Amours et al. 2001; Smith and King 2005). The transition from drifting as free embryos to settling as larvae is likely dependent on a suite of temperature-dependent processes involving larval development, yolk sac absorption, and the transition from endogenous to exogenous feeding. For pallid sturgeon, results suggest that the transition from drifting to settling occurs through a range of length and development, where the settling process is initiated at about 18 mm and completed at about 20 mm (Braaten et al. 2008).

Extended downstream drift and dispersal of pallid sturgeon free embryos resulted in greatly expanding time-of-travel catch distributions as post-release duration and distance increased. Similar patterns have been reported for free-drifting pallid sturgeon and shovelnose sturgeon in a Missouri River side channel (Braaten et al. 2008) and in hydrologic investigations where passively drifting dye particles have been used to determine travel time and dispersion patterns (Kilpatrick and Taylor 1986; Jobson 1997). Related to time-of-travel, drift velocities of pallid sturgeon free embryos decreased as drift distance increased. Whereas interactions involving larval behavior and channel hydraulics contributed to only slightly slower drift velocities relative to water velocity at the 5.7 km location, increasingly slower drift velocities with increasing drift distance likely reflected improved swimming abilities of developing free embryos and increased exposure to channel heterogeneity and hydraulic conditions. Specifically, free-drifting life stages during a prolonged drift period experience increased encounters with eddies and other habitat features (e.g., sand bar pools) that briefly entrain a portion of the population prior to re-entry into the main channel flow field (Kynard et al. 2007). Cumulative exposure to these conditions during a prolonged duration of downstream drift and dispersal would gradually reduce downstream transport velocity. Manifestation of this process was most evident on 12 July when cumulative reductions in drift and dispersal velocity slowed the drifting population, resulting in the lack of free embryo occurrence in the drift.

Cumulative drift distance

Empirical data and cumulative drift models indicate that pallid sturgeon free embryos exhibit an extended drift and dispersal period during ontogenetic development, where downstream dispersal may persist for 8–14 days depending on water temperature and development. In addition, although pallid sturgeon exhibit active behaviors during the downstream drift and dispersal period, high velocities characteristic of large river channels result in net downstream transport of free embryos and disperse pallid sturgeon several hundred km downstream from spawn and hatch locations. Earlier laboratory studies suggested that pallid sturgeon drift about 13 km during ontogenetic development when subjected to low test velocities ($\leq 0.12\ ms^{-1}$; Kynard et al. 2002a) and in excess of 300 km at greater test velocities ($\leq 0.30\ ms^{-1}$; Kynard et al. 2007). In small-scale field studies, Braaten et al. (2008) modeled an 11-day cumulative drift distance as a function of water velocity and suggested that the average pallid sturgeon free embryos may drift 245 km at 0.30 ms^{-1} and 530 km at 0.60 ms^{-1}. Incorporating long-distance drift characteristics and hydraulic elements in the mainstem Missouri River, drift distance models from the present study provide more definitive inferences on cumulative distance drifted by pallid sturgeon during ontogenetic development than earlier studies. In addition, results clearly demonstrated that cumulative drift distance based on passive transport of free embryos drifting at mean velocity exceeded cumulative drift distance based on interactions involving behavior, water temperature, age- and size-related variations in drift rates, and channel hydraulic characteristics. Thus, models of passive transport based exclusively on mean velocity will over-estimate cumulative drift distance of larval pallid sturgeon.

Similar to pallid sturgeon, evidence for long-distance dispersal from spawn and hatch locations is available for other acipenserids with pelagic larvae. For example, Siberian sturgeon *A. baerii* may disperse in excess of 400 km during the first few days of drift (Gisbert and Ruban 2003) and white sturgeon *A. transmontanus* in excess of 150 km (McCabe and Tracy 1994). Mechanisms contributing to or the benefits derived from a long-duration, long-distance mode of dispersal are not specifically known in pallid sturgeon but may include several considerations. First, initiation of downstream dispersal immediately after hatching has been proposed as a mechanism to enhance survival when predation risk is high at spawn and hatch locations (Kynard and Horgan 2002; Kynard et al. 2002a, b). Whereas this explanation is intuitive for explaining immediate dispersal from the hatch location, long-duration and long-distance dispersal of free embryo pallid sturgeon implies that the risk of predation remains high for several hundred km downstream from historic spawn and hatch locations in the Missouri River. Drifting by free embryos in the highest velocity regions of the channel (this study; Braaten et al. 2010) would facilitate dispersal from areas of high predation risk, and minimize stranding or settling in slow water habitats where predation risk may be high (Kynard et al. 2007). Second, an extended larval drift duration and distance may serve as a mechanism to transport free embryos from coarse substrate spawn and hatch areas to downstream sand-dominated areas that provide suitable foraging and rearing habitats for young (Kynard et al. 2002a). For example, except during the spawning season, coarse substrates are infrequently used by pallid sturgeon as free embryos and larvae do not reside in cover (Kynard et al. 2002a, 2007) and juvenile and adult pallid sturgeon prefer sand substrates (Bramblett and White 2001; Allen et al. 2007). Plausibility of this explanation rests on the assumption that several hundred km of coarse substrate habitat occurred between historic spawning and rearing locations in the upper Missouri River basin prior to anthropogenic alterations.

Cumulative drift models for all temperatures and drift durations showed a range of distances drifted by the population under a specific velocity condition; this range reflected population-level variations in drift velocity relative to water velocity exhibited by free embryos during the downstream drift and dispersal period. Across all velocities, this pattern would distribute pallid sturgeon through a broad range of river locations as reported in white sturgeon (McCabe and Tracy 1994) and Chinese sturgeon A. sinensis (Zhuang et al. 2002) that exhibit downstream dispersal behavior. For example, pallid sturgeon free embryos drifting at a mean velocity of 0.70 ms^{-1} for 10 days (20°C) would settle over a 204 km reach of river (minimum=256 km, maximum=460 km, mean=383 km). Transitioning from drifting to settling across a broad reach of river is an effective strategy to minimize competition for food resources (McCabe and Tracy 1994; Gisbert and Ruban 2003) when food acquisition during the switch from endogenous to exogenous feeding is an important factor for growth and survival (Gisbert and Williot 1997; Gisbert and Doroshov 2003).

Empirical data and cumulative drift models developed in this study provide inferences on a mechanism for the lack of recruitment by pallid sturgeon for the last several decades in the upper dam-fragmented upper Missouri River. Specifically, the prevailing hypothesis for lack of recruitment is based on the premise that there is an insufficient length of free-flowing riverine habitat available to free-drifting live stages of pallid sturgeon between hatch and settling locations (Kynard et al. 2007; Braaten et al. 2008), and that conditions in reservoirs at the drift terminus are not suitable for survival of free embryos or settling larvae (Kynard et al. 2007). Two examples lend support to this hypothesis based on drift models developed in this study.

First, pallid sturgeon are suspected to spawn in the Yellowstone River approximately 12–14 km upstream from the confluence with the Missouri River (Bramblett and White 2001; Fuller et al. 2008). This distance, when combined with an additional 25 km of free-flowing Missouri River between the confluence of the Yellowstone River and headwaters of Lake Sakakawea at full pool, results in a total length of about 37 km of free-flowing river. Under relatively natural conditions in the Yellowstone River (White and Bramblett 1993; Bowen et al. 2003) and warm water temperatures during the spawn and drift period (18–24°C; Fuller et al. 2008; Braaten et al. 2009b), the drift distance required by free embryos greatly exceeds available drift distance under all modeled temperature and water velocity scenarios.

Second, about 340 km of free-flowing river occurs between Fort Peck Dam on the Missouri River and the headwaters of Lake Sakakawea. Hypolimnetic releases through Fort Peck Dam suppress water temperature, and the initial 40–50 km below the dam are likely too cold to support spawning by pallid sturgeon. Downstream from this point, water temperatures of at least 14–16°C occur during much of the late-spring and early summer spawning season (Braaten et al. 2009b). Thus, if spawning by pallid sturgeon occurs in this portion of the Missouri River, about 290–300 km of free-flowing river would be available for larvae to complete ontogenetic development prior to reaching the headwaters of Lake Sakakawea. The cumulative drift model based on 14°C (14 day drift period) predicts that the population of free embryos would drift a minimum of 307 km to a maximum of 547 km at mean water velocities of 0.70 ms^{-1}. At 16°C (13 day drift period) and a mean water column velocity of 0.70 ms^{-1}, predicted drift distance ranges from a minimum of 295 km to a maximum of 528 km. Under both scenarios, results strongly suggest that pallid sturgeon drift requirements exceed the available length of free-flowing riverine habitat. Although there is the possibility that some of the slowest drifters in the populations would settle prior to reaching Lake Sakakawea and survive, available data do not support this hypothesis as there has been no evidence of recruitment in this population for decades.

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